

A GENETICIST'S VIEW OF HOBBYISTS GUPPY STRAINS.

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In nature, guppies occur as isolated and semi-isolated local populations in still waters such as ponds and drainage ditches, and in slowly moving streams. Fish from one population or habitat may occasionally enter a different population or habitat by natural means (migration, or even being dropped by a predatory bird!) or more frequently as the result of human intervention. Indeed the guppy's fame as a predator on mosquito larva has led to its intentional dissemination throughout much of the tropical and subtropical world.

In 1963, Ernst Mayr published his book, Animal Species and Evolution. By doing so, he set off an explosion in the world of evolutionary biology and population genetics. The details of his proposals are still being fought over almost 50 years later. But much of what he said has been proven to be essentially correct. Mayer proposed that a local population (a deme) contains within it a collection of genes (a gene pool) that interact harmoniously with each other to produce a healthy product that is well adapted to the local environment in which the population is found. These genes form coadapted gene complexes as a result of selection that acts upon the various expressions of the genes, and modifies the expression or eliminates those genes that do not interact well together, while increasing the frequencies of those genes that do interact well together.

Therefore when we think of wild guppy populations, we may imagine a mosaic of demes within a large geographical area. Each deme adapted to its own peculiar set of environmental conditions, yet often maintaining some level of gene flow with other such demes. If instead, we think of guppies in hobbyists tanks, we find a very similar situation. Each strain may be isolated from the others as if it occurred in a different pond in nature. Migration may occur between these strains either due to the hobbyist's deliberate actions, or when a fish jumps from one tank to another. Fish migrate from owner to owner.

WHAT IS A PURE BRED STRAIN?

As guppy hobbyists, we maintain local populations of one or more strains of guppies. Thus we employ artificial selection to create a population of inbred guppies that has been selected for certain characteristics that we consider important, such as fin size and shape, the presence or absence of certain colors, etc. These populations become adapted to our local water conditions (pH, hardness and calcium content, temperature range, foods). As the population becomes better adapted to our local conditions, and subject to our artificial selection, it tends to lose some of its initial genetic variability due to selection, inbreeding (mating of close relatives) and genetic drift (changes in gene frequency over time due to chance alone). Over generations, the members of the population become more uniform both physically and genetically. The resultant inbred strain is more genetically uniform and therefore more phenotypically uniform as well. It is homozygous for many loci. All males will be similar to each other, and all females to each other as well. Unfortunately as the population continues to lose genetic variation, it also is likely to lose some beneficial genes by chance alone simply due to genetic

drift (caused by things such as a small number of breeding individuals, a small number of ancestors, the loss of a desirable gene that is closely linked to one that we are selecting against, etc.) Many of the less desirable traits that remain are due to homozygous mutant recessive genes. In nature the harmful effects of inbreeding depression in a particular deme, with its loss of desirable genes and gene combinations due to drift, may be compensated for by migration into the population of the lost genes carried by immigrants from other populations. The breeder mimics this when he/she maintains several lines of a strain and established crosses between them. The breeder may also obtain related fish from another breeder, again reducing the possible harmful effects of inbreeding and drift.

WHY DOES THE F_1 FROM UNRELATED STRAINS OFTEN LOOK VERY GOOD (OR BAD)?

When we do an outcross, we mate individuals from two inbred strains to each other, and mimic a migration event as mentioned above. (Actually, we mate two unrelated individuals, even if one is not from an inbred strain. But crossing to an individual that is not from an inbred strain adds much more genetic variation and we may find the results disappointing.) If the two parental strains are very closely related, the P_1 , F_1 and later generations may not be very different from each other. But with luck or as the result of previous experience we may find that some dominant desirable alleles from one strain are introduced to replace lost alleles and “cover up” (are dominant to) the effects of the less desirable recessive alleles of the other strain. This is the basis for line breeding schemes such as have been described by various authors. Thus we regain desirable genes that were lost as a result of inbreeding. It often surprises readers when they find that the effect of genetic drift due to small breeding population size is stronger than all but the strongest levels of artificial and natural selection! We can lose treasured genes and resultant phenotypes from a mixed population due to drift in spite of our attempts to select in their favor. This may be why some breeders prefer to use groups of breeders instead of single pairs when maintaining a line of fish.

If we do an outcross using unrelated strains, even though they may appear phenotypically similar in many ways, this apparent similarity is likely to be deceptive. Each will have a different coadapted gene pool. Each strain may have long delta tails, but the individual genes that produced these caudal fins (or dorsal fins, or fin color, etc.) may be due to different combinations of alleles in each case. The F_1 will be heterozygous for each of the pairs of genes in which the parental strains differ from each other. In some cases, the F_1 will be phenotypically superior to the pure bred members of either parental strain. The dominant alleles from each strain “hide” the effects of the recessive less desirable alleles from the other strain. This is sometimes referred to as “hybrid vigor” or “heterosis”. (The F_1 may combine the worst characteristics of each strain instead, but no one brags about those results!)

A well known guppy breeder and judge recently said that his F_1 s from certain crosses have won prizes in IFGA competitions. But as he and others have also observed the F_2 phenotypes from these crosses are often so poor that they are completely culled out by the breeder. This is because each heterozygous pair of genes segregates independently from each of the other pairs of genes in the F_2 . A “hybrid swarm” of new genotypes and phenotypes is produced. Many individuals are genetically

different from the others. Most of them are still heterozygous for many pairs of genes. Hybrid breakdown results in the breakup of the coadapted gene complexes as well. Viability and suitability for a given environment may vary. So did these glorious F_1 fish really deserve the praise heaped upon them, when they cannot and will not breed true and produce a population uniformly like themselves? That must depend upon the philosophy of the breeder's club members. Someone answered this point before I even published this article, when they stated on-line (and then deleted it) "It is great if you enjoy guppy genetics or creating unique strains, but IFGA members want to produce the most colorful, biggest, best balanced and best finned fish we can get on the bench, AKA big ass show stoppers!!!" I partially agree with them. I also want to produce these wonderful fish, but I want them to breed true. If I buy a winning fish at a show, or from a show breeder, I want its descendants to be like it. I definitely wouldn't waste my money to buy a "one shot wonder"!

ARE F_1 HYBRIDS EVER DESIRABLE ON THEIR OWN MERITS?

There is an instructive example from the U. S. corn breeders that I used to teach to my Genetics students. The corn breeders have produced highly inbred, highly homozygous strains of corn. These inbred strains often don't look like anything that you or I would want to plant or eat. They may be short, have small ears, few kernels per ear, etc. But, the breeders already know from prior experience, that if they cross strain "A" and strain "B", the F_1 will produce large ears filled with many uniformly sized sweet kernels. The seed company maintains the pure strains of corn. They cross the two strains together and sell the F_1 seeds to the farmer. The farmer raises tons of F_1 corn and sells its seeds to the public. If the farmer or his customer plants the F_2 kernels (seeds) produced by the F_1 plants, they are deeply disappointed when they find that hybrid breakdown has occurred in the F_2 and most of the ears of corn are not nearly as beautiful as was the F_1 . So each year the farmers return to the seed company and buy more F_1 hybrid corn to raise and market. I have heard that some mass producers of guppies for the pet shop trade follow the same practice and sell hybrids that will not breed true. I do not know if this statement is valid or not. Apparently some guppy breeders may sometimes use similar techniques to produce prize winning guppies.

HOW ARE THE F_1 USEFUL TO A BREEDING PROGRAM?

If you see some traits in a different guppy strain that you feel might improve your guppy strain, then the best way to do this would be to establish the second strain in your fish room. Breed them for a few generations and select ones that do well under your environmental conditions. You now have two separate strains. You continue to maintain these two separate populations while you initiate crosses between them. Rather than repeat what has already said by other authors, I will only add some comments. Instead of breeding the F_1 together and getting an F_2 , F_3 , etc. complete with hybrid breakdown, you follow a backcross scheme instead. You obtain the F_1 . You cross a highly desirable F_1 fish back to a member of one of the two pure strains. From this cross, you obtain the BC_1 (first backcross generation). You cross a highly desirable BC_1 fish back to a member of the pure strain. You continue to do this until the broods that you get are uniform and express the trait(s) that you were transferring into the uniform genetic background of the original strain. How does this work? If you cross strain A x strain B,

the initial F_1 has 50% ($\frac{1}{2}$) of the genes from each parental strain. Each time you backcross, you further multiply this by another $\frac{1}{2}$. So the offspring of the first backcross generation (BC_1) from the cross of the F_1 x strain A will contain $(\frac{1}{2})(\frac{1}{2}) = \frac{1}{4}$ of the genetic makeup of strain B. The BC_2 will have $\frac{1}{8}$ of the genes from strain B, etc. If guppies have approximately 20,000 pairs of genes, the $\frac{1}{8}$ of that is still 2,500 pairs of genes. But many of the genes were essentially the same in the two populations to begin with, so the degree of difference is theoretically less than that. Why “theoretically”? Because natural selection and drift may counteract your efforts as a breeder and the resultant population may be less homozygous than you think. Transferring one or several genes from one population into another population without otherwise changing the genetic makeup of the second population is referred to as introgression.

IS IT HELPFUL TO KNOW HOW THE TRAIT IS INHERITED?

Not only may it be helpful, it may be necessary! Let me give an example. We know that the Moscow gene is Y-linked and does not cross over to the X chromosome. If we want to develop a strain that combines the Moscow gene from strain A and the fin size from strain B. We will have to use a male from the Moscow strain A because if we use a female from strain A, she will not have the Moscow gene! Since fin size and shape probably involve more genes than does the Moscow gene and any of its modifier genes, we may decide to backcross the F_1 male into the strain B that already has all of the required genes for finnage. We will only have to add a single gene from our Moscow strain. In each generation, we will have to cross our best Moscow hybrid male back to strain B females. Since the quality of Moscow expression will be important, we will want to select for the quality of this character in each generation.

If you don't know if the trait is due to a sex-linked gene, and if so whether the gene is X-linked or Y-linked (or both!), you need to do reciprocal crosses. That means that in one set of crosses you use males of strain B and females of strain A. In the reciprocal cross, you use males of strain A and females of strain B. You compare the F_1 males with each other and the F_2 males with each other. (Assuming you are interested in a male trait.) If the trait is X-linked, it is transmitted from mother to sons (and daughters). If the trait is Y-linked, it is transmitted only from father to sons, to grand sons, etc. it is transmitted only through males and never through females. If the trait is autosomal and dominant it is present in the F_1 males from both crosses and most F_2 males from both crosses. There are other possibilities, but they are outside of the scope of this article and have been discussed by other authors such as Philip Shaddock (2010) in The Theory and Practice of Guppy Breeding.

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